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Advances, diversions, possible relapses and additional problems in understanding the early evolution of the Articulata

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ABSTRACT

The authors review the available evidence concerning the early stages of radiation of the Articulata and support the hypothesis that there was probably a range of, perhaps incompletely, metameric organisms spanning, without definite borderlines, the early ancestors of arthropods, lobopods and annelids. By the early Cambrian, the stem lineages of the living articulate phyla were well-identified, but there still survived a number of animals whose morphology spanned, to some extent, the gaps between the living taxa. The affinities between Annelida (*sensu lato*) and Mollusca are briefly discussed.

KEY WORDS: Articulata - Evolution - Morphology.

ACKNOWLEDGEMENTS

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1. INTRODUCTION

As even the very existence of the Articulata, by which is meant that group of phyla presently including the Annelida and the Arthropoda, as well as several minor groups that show a metameric and gastroneuralian Bauplan, has been challenged, it might, perhaps, be worth while to justify briefly our more traditional approach.

In the last years, a wealth of new and diverse evidence has been produced concerning the phyla grouped under the Articulata and there is no doubt that this evidence has to be assessed within a coherent framework. This is presently difficult for three main reasons: (1) when such evidence is apparently conflicting, each scholar usually not only chooses which should be given more credit, but also defends it vigorously, while it should be apparent that when two different lines of evidence apparently support conflicting hypotheses, then we should ask ourselves why that should be so; (2) to compound the difficulties, the problems are usually tackled by conflicting methods, and it is unavoidable that apparently irreconcilable evidence analysed by conflicting methods will produce grossly incompatible results¹; (3) palaeontologists and morphologists on the one hand, and molecular and experimental biologists on the other, are all too often insufficiently aware of the serious limitations of their own evidence and, even more so, of the evidence provided by colleagues in other fields.

The assumption that the study of DNA and RNA is providing the 'final' answer to phylogenetic problems (Ishikawa, 1977; Hewett-Emmett *et al.*, 1982; Cann *et al.*, 1987; Van Le *et al.*, 1989; Swofford & Olsen, 1990; Christen *et al.*, 1991) is definitely useful in so far that it prompts the discovery of new and certainly significant evidence, but it is still an assumption that only a much larger range of data may eventually prove; this is because there are also theoretical reasons which suggest that convergences, changes in rates and times of change in the genomes may well blur the picture, just as happen with the more classical morphological evidence (Carlson *et al.*, 1978; Kluge, 1983; Felsenstein, 1988; Schmid & Marks, 1990; Hillis & Moritz, 1990; Bledsoe & Raikov, 1990; Danieli & Fracasso, 1991).

We shall, therefore, limit ourselves to considering the morphological and palaeontological evidence by the standard methods of comparative anatomy, while some further discussion of this point will be embarked on in the concluding remarks.

However, a point that must be stressed beforehand is the following: our understanding of the early evolution of the basic Bauplans rest largely on the fossil evidence, but although excavations are providing literally thousands of specimens every year, their publication is

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¹ - For the sake of space, it is impossible to discuss here the reasons of our scepticism towards the methods of cladistic analysis; the reader is therefore referred to Simonetta 1992, 1993, 1996.

painfully slow and most of the fossils lie in museum trays so that their very existence is not known. That the scholars engaged in the excavations want to keep to themselves such materials as are specially relevant for their own researches is quite understandable, but, as the wealth of material being excavated clearly exceeds the possibilities of study of any individual, it is highly desirable that, after a preliminary gross sorting, lists of all the materials be made available, so that scholars engaged in any particular field may know where to look for specimens which will possibly be significant for their own researches. We shall see, further on, some specific examples of such problems.

1.1 Annelida

So far, only the Burgess Shale Middle Cambrian Annelida have been revised (Conway Morris, 1979). Although some supposed annelids have been removed from allocation to this phylum, there remains a hard core (*Burgessochaeta*, *Canadia*, *Insollicorypha*, *Peronochaeta*, *Stephanoscolex*) of unquestionable Polychaeta. They are all jawless, just as in different living families, the occurrence of jaws being by no means typical for polychaetes. However, it may well be arguable whether, in living annelids, the lack of jaws should be considered as a primitive feature or as being due to secondary loss (actually the earliest scolecodonts appear during Ordovician times): for instance it is probable, but not certain that the Clitellata evolved directly in

brackish waters from jawless Cambrian Polychaeta (Fig. 1). These worms were typically metameric and were provided with rather well-developed parapodia, though their details are unclear. Other possible Cambrian annelids have been described, but their status is more doubtful.

A brief mention may be made here of the *wiwaxiids* and *halkieriids*. *Wiwaxia* was originally considered as a Polychaeta by Walcott (1911b), but Conway Morris (1985), having noticed the peculiarities of these animals, suggested that they should be considered as being the representatives of a separate phylum. Butterfield (1990), instead, having shown how similar were the spines and scales of *Wiwaxia* to the paleae of some annelids, suggested that these animals were close relatives of the Chrysopetalidae and Aphroditidae. However, in order to defend this conclusion, Butterfield was obliged to argue that the oral apparatus described by Conway Morris was rather like polychaete jaws and not a sort of primitive radula, making *Wiwaxia* the earliest jawed polychaete. Not having studied the material, we have to rely on published evidence and it appears to us that indeed the animal was provided with a radula-like apparatus rather than with jaws. On the other hand, the living Caudofoveata, another puzzling group, which could equally well be considered as a primitive "sister group" to all Molluscs or as an extremely specialised group with affinities with Bivalvia (on developmental evidence) are provided with paired structures resembling jaws rather than with a radula.

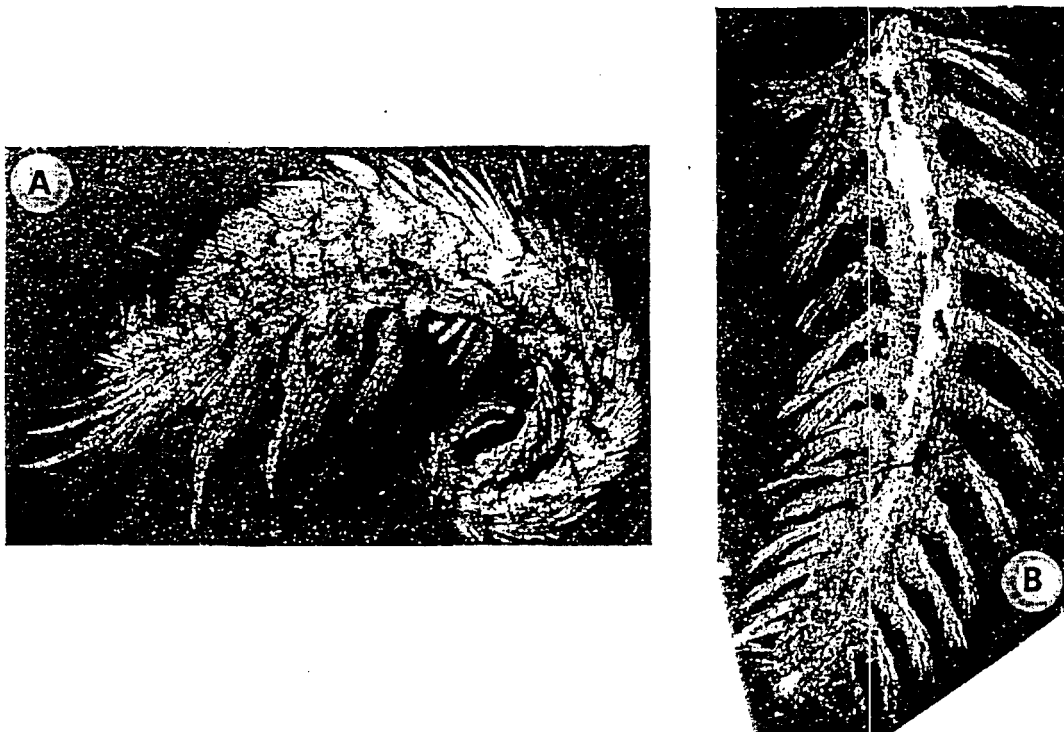


Fig. 1 - Two Middle Cambrian Polychaetes from the Burgess Shale: A, *Canadia spinosa* Walcott, 1911, (USNM 83929d); B, *Burgessochaeta setigera* (Walcott, 1911) (USNM 83930b)

Equally puzzling are the Halkieriids: from what is known they may be related to primitive molluscs, especially to Aplacophora and Placophora, but close relationships to the Brachiopoda have also been suggested (Conway Morris & Peel, 1990, 1995).

Again, if the presence of Bivalvia in the lower Cambrian is definitely proven (Jell, 1980; Wang Bing, 1994), true advanced molluscs must have occurred at extremely early times, but they were accompanied by a range of other trochozoans which nicely spanned the gap between the true annelids and the typical molluscs.

We shall leave here the Annelida, as it is well known that the phyletic relationships of most groups are far from clear and some recent proposals based on cladistic analysis (Nielsen, 1995) rest on questionable assumptions. As for the recent theories by Shcherbakov (in press), who suggests a direct relationship of the Arthropoda and related groups to the Polychaeta, and especially to animals like the Aphroditacea, we have only a summary distributed in London in 1996 and, therefore, we cannot give a proper comment on them.

1.2 Tardigrada and Linguatulida

Though Tardigrada are, as yet, an insufficiently studied group and especially the marine tardigrades have been studied, so far, mainly for primarily taxonomic purposes, yet everyone is well aware that their systematic position has long been hotly debated. Recently Müller *et al.* (1995) have described an unquestionable, well-preserved member of Tardigrada from the Cambrian of Siberia (Fig. 2A-E). A peculiar and significant feature of this animal is that, apparently, it had an anamorphic development. The only specimen described (additional specimens have recently been recovered) has only three pairs of legs with possible evidence of a fourth developing pair. It is also interesting to note the lateral direction of the appendages, although the possibility cannot be entirely ruled out that this is due to a slight post-mortem distension of the specimen, mainly affecting the ventral side, which was obviously more flexible.

Considering now: (1) the morphology of the Cambrian animal; (2) the fact that is not known whether the cuticle of living tardigrades is composed of α - or β -chitin (Crowe *et al.*, 1970, 1971a, b; Baccetti & Rosati, 1971; Bussers & Jeuniaux, 1973a, b; Greven, 1971a, b, 1972, 1975; Schuster *et al.*, 1975; Karuppaswamy, 1977 - but on this last see the Appendix); (3) that the development of mesoderm and coelom as traditionally related (Marcus, 1929) has been challenged (Nielsen, 1995); (4)

that molecular data on rRNA give highly controversial results: while Giribet *et al.* (1996) find affinities with the onychophorans and arthropods, Moon & Kim (1996) claim that, though excluding affinities with "aschelminths *s.l.*", data indicate the tardigrades as a sister group of all the remaining protostomes (Nemertea, Sipuncula, Annelida, Arthropoda). Thus, at least the argument for affinities of tardigrades with aschelminths (Crowe *et al.*, 1970; Dewel & Clark, 1973; Bergström, 1986; Hou *et al.*, 1995) should be rejected. Indeed, just a few months ago Dewel & Dewel (1996, in press) argued at the London International Symposium on the Evolution and Relationships of Major Arthropod Groups (Fortey and Thomas, 1998), that there is now strong evidence for the affinities of the Tardigrada, Onychophora and Arthropoda, and that most peculiarities of Tardigrada are related to their minute size. Moreover, as characters assumed to be synapomorphies have all a clearly adaptive significance for minute animals basically belonging to the meiofauna (for criticism on the hypothesis of aschelminths affinities see Nielsen, 1995), there is a strong presumption that they are the result of convergent evolution of some apparatuses. There is anyway no doubt that an intensive study of the marine tardigrades will produce rewarding results (Fig. 2F-G).

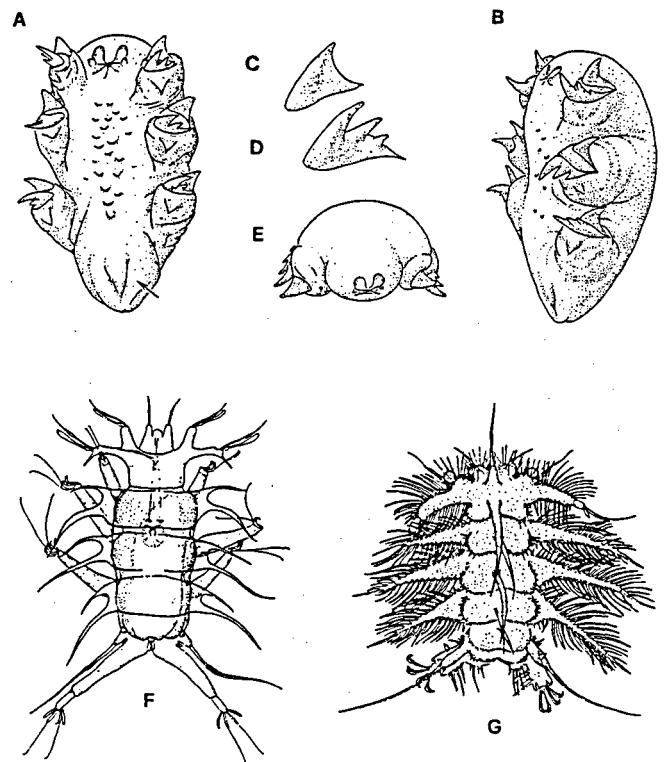


Fig. 2 - The Cambrian Tardigrade as figured by Walossek (1995). A, ventral view; B, lateral view; C, fore hook; D, hind hook; E, frontal view of the animal; F, the living marine *Parastygarctus bigginsi* Renaud-Debyser, 1965; G, the living marine *Neostygarctus acanthophorus* Grimaldi De Zio *et al.*, 1982: note the spiny surface of these animals, superficially similar to that of some Cambrian Lobopods proposed in Figure 5.

Rudall (1963) affirms that all three chitins (α - β - γ) may occur together in the same animal, but in different tissues and recent data (Riley & Banaja, 1975; Riley *et al.*, 1978) have cast some doubts on a substantial difference between cuticles with α - or β -chitins; apparently they are usually both present, but in radically different proportions, α -chitin being prevalent in Onychophora and Arthropoda, β -chitin in Annelida and Pentastomida (this last record, however, requiring verification).

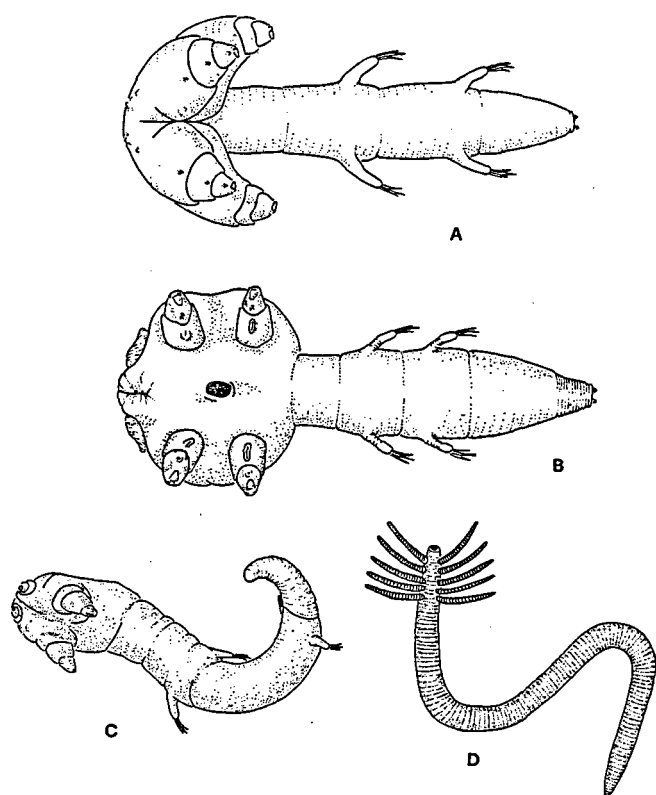


Fig. 3 - Some of the Upper Cambrian Pentastomids. A, *Heymonsi-cambria scandica* Walossek & Müller, 1994; B, *Boeckelericambria pelturae* Walossek & Müller, 1994; C, an advanced larva (after Walossek & Müller 1994); D, the enigmatic Lower Cambrian *Facivermis yunnanicus* Hou & Chen, 1989, a possibly distantly related species.

Coming now to consider the Linguatulida (or Pentastomida), new data have destroyed some phylogenetic hypotheses which have been proposed, even rather recently (Riley *et al.*, 1978; Böckeler, 1984; Abele *et al.*, 1989, 1992; Storch & Jamieson, 1992).

Walossek & Müller (1994) and Walossek *et al.* (1994) have described from different European and American Cambrian localities rather diverse pentastomid larvae (Fig. 3A-C), and compared them with living ones (Fig. 4). As one can easily see, and as Walossek himself stressed, we had already in the Cambrian two clearly different, though rather primitive, groups of pentastomids. In one of them, apparently, the larval stage had no mouth, while primitive features are, for instance, obvious in the more "arthropod-like" appendages. It is notable that even at that early age the Pentastomida were clearly parasites; Walossek suggests that they may have been parasitic in the pallial cavity or inside the valves of animals like some arthropods, brachiopods or molluscs.

The combined evidence obtained from these larvae and the chitinous composition of living pentastomids, basically β -chitin whose prevalence is typical of annelids (see Karuppaswamy, 1977, if true), disposes of such hypotheses as those maintained by Wingstrand

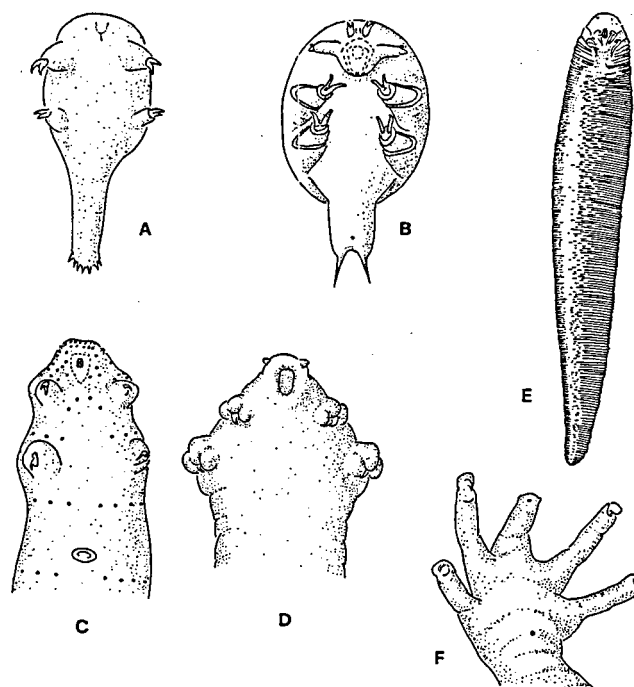


Fig. 4 - Some living Pentastomids for comparison with Figure 3. A, *Pentastomum taenioides*; B and D, *Raillietiella kochi*; C, *Reighardia sterna*; E, *Linguatula multiannulata*; F, *Cephalobaena tetrapoda* (all from Walossek & Müller, 1994).

(1972) and by others, who suggested affinities to crustaceans, especially Branchiura; this hypothesis was based on similarities of the spermatozoon and on some developmental features (Storch & Jamieson, 1992). Even if we consider Karuppaswamy's report as suspect, the Cambrian pentastomid larvae are contemporary to faunas which clearly show that the lineage or lineages that evolved into typical Crustaceans, while they had undoubtedly begun to acquire the typical crustacean characters by the Lower Cambrian, by Upper Cambrian times had not yet achieved their whole set. Thus, as the Pentastomida must have separated from other lineages at least from the Middle Cambrian, they cannot possibly belong to the same lineage as the Branchiura (Argulids), which, being typical, albeit specialised crustaceans, must belong to a lineage which originated much later from a more typical crustacean stem.

As far as the peculiarities of the sperms are concerned, the works, for instance of Baccetti, Baccetti & coll., Dallai and Dallai & coll. etc., totalling several dozens (extensive and updated accounts of the more general evidence may be found in Jamieson *et al.*, 1995), clearly show that the spermatozoa of Arthropoda underwent an extraordinary variety of specializations and apparent convergences and parallel developments, so that their evidence, though far from irrelevant, must in each case be assessed by comparison with all other types of evidence. Much the same can be said of embryological evidence as it is apparent, when all that is

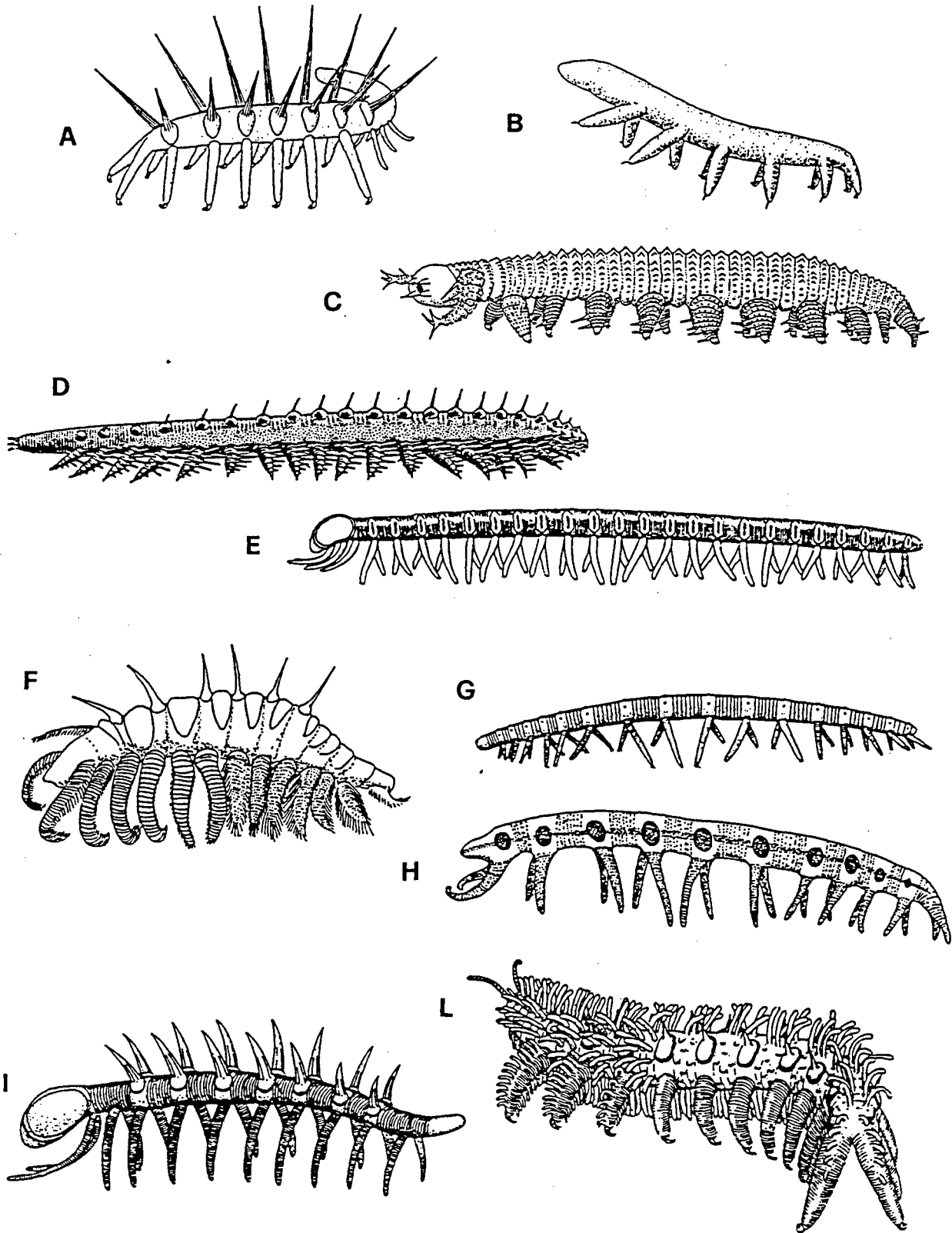


Fig. 5 - The better known Cambrian Lobopods. A, *Hallucigenia sparsa* (Walcott, 1911) (Middle Cambrian); B, *Paucipodia inermis* Chen *et al.*, 1994 (Lower Cambrian); C, *Aysheaia pedunculata* Walcott, 1911 (Middle Cambrian); D, *Xenusion auerswaldae* Pompeckj, 1926 (Lower Cambrian); E, *Cardiodictyon catenulum* Hou *et al.*, 1991 (Lower Cambrian); F, the unnamed animal of Collins, 1986 (Middle Cambrian); G, *Loulishania longicruris* Hou & Chen, 1989 (Lower Cambrian); H, *Microdictyon sinicum* Chen *et al.*, 1989 (Lower Cambrian); I, *Hallucigenia fortis* Hou & Bergström, 1995 (Lower Cambrian); L, *Onychodictyon ferox* Hou *et al.*, 1991 (Lower Cambrian). A after Ramsköld (1992); B original; C, D, F after Delle Cave *et al.* (1991); E, G-L after Hou *et al.* (1995).

available on it is compared with other kinds of evidence, that its significance is highly variable from group to group.

It is clear, as far as available evidence goes, that Pentastomida, Tardigrada and Onychophora do not really bridge the hiatus between the more arthropod-like phyla and the Annelida, but form with the more typical arthropods a swarm of related groups, which show a sort of cocktail of variously assorted characters which cannot be ordered in a definite pattern, but rather suggest the past existence, probably at the transition between the Precambrian and the Cambrian, of a wide and almost continuous range of mixed possibilities, that by the times of the Chinese Lagerstätte had already been reduced to about half a dozen lineages.

1.3 *Onychophora and related taxa*

During the past few years, the range of lower Cambrian taxa more or less closely related to the living onychophorans has greatly increased, while a few additional Middle and Upper Cambrian and later onychophoran-like animals are now known (Ramsköld & Hou, 1991; Hou & Bergström, 1995) (Fig. 5). All these forms and the living onychophorans are generally included in a taxon Lobopoda, following our suggestions of 1981 (Simonetta & Delle Cave, 1981). A few years ago, the Indian zoologist Sundara Rajulu claimed to have discovered a living marine lobopodan; this is a strange story, which is fully related in the Appendix.

Although not all the Cambrian Lobopoda sport spines or other sclerites, the majority do, and this points to two features in their mode of life: (1) the need for protection against predators, and, indeed, a whole range of probable predators are known from the same localities which have yielded the lobopodans, (2) most have rather long and thin legs, at least in comparison to modern onychophorans. Such legs might work in a marine environment, where gravity was largely counteracted by water density.

Developing Whittington's (1978) argument for *Aysheaia* living mostly among sponges, we may suppose that the spiny lobopods lived in more open waters, while animals like *Paucipodia* and *Aysheaia* lived either in crevices, or among or even inside sponges and sponge-like organisms. It is remarkable that some living marine tardigrada have a spiny tegument closely resembling that of some Cambrian Lobopoda, while again *Paucipodia*, with only six pairs of legs appears intermediate (size apart) between the Lobopoda and the Tardigrada (and it is notable that Dewel & Dewel (1996) consider that the head region of Tardigrada includes three metameres, so that the whole body of the Tardigrada should actually consist of six postoral segments).

Research on living Tardigrada is producing evidence to the effect that these animals were originally dwarfed marine lobopodans (Budd, 1996; Dewel & Dewel, 1996), whereas the Onychophora became terrestrial and

consequently modified their skin the better to negotiate crevices and bark.

The mixed nature of the Carboniferous Mazon Creek fossils (some being obviously aquatic, while others were terrestrial animals which became entombed in shallow waters) does not allow us to decide whether the remarkably *Peripatus*-like *Helenodora inopinata* (Thompson & Jones, 1980) was still an aquatic animal. Anyway, obvious mechanical requirements suggest that both in the arthropods and in the onychophorans the significance of hydrostatic pressure for the extension of the legs became less important than it was in the Cambrian animals, and such reduction went parallel with an increasing complication of the leg musculature in both groups.

Several authors (Briggs *et al.*, 1993; Wills *et al.*, 1994) have commented on the variety of Cambrian Lobopoda, even within a single Lagerstätte. Indeed, they appear to be all independent, though more or less closely related, radiations from a common source. Actually, apart from the differences in size and number of the appendages and the dorsal spines, the significant differences are: (1) the probably respiratory papillae of *Onychodictyon*; (2) the fact that some genera, like *Aysheaia*, and the Tardigrada, have the anus at the attachment of the last pair of legs, while others have an anal papilla like that of modern onychophorans, (3) in the formally unnamed "Collins' monster" there is a single row of dorsal spines instead of the two seen in other spiny genera, and the legs appear to be divided into two morphologically different groups (but that might be due to peculiarities in fossilization); (4) finally, *Microdictyon*, formally described by Ramsköld & Hou (1991), but whose sclerites have long been known from several localities, instead of being armoured with spines, had a series of curious perforated platelets.

The lower Cambrian *Facivermis yunnanicus*, described by Hou & Chen (1989) (Fig. 3D) has been variously interpreted: some authors (Hou & Bergström, 1995) hold that its appendages have the nature of tentacles and that, therefore, its should be considered as a kind of "worm", while others, including ourselves (Delle Cave & Simonetta, 1991) have suggested that it may be related to the Lobopoda. Now that Cambrian Pentastomida are known, it might also be suggested that *Facivermis* may be a scavenger, more or less closely related to the pentastomids, in spite of the fact that it has a greater number of forelegs and apparently lacks the rudimentary abdominal ones occurring in the Cambrian pentastomid larvae (Fig. 3).

Three main problems remain to be investigated: (1) the significance of the differences in cuticle structure in Tardigrada and Onychophora, with the proviso that, considering the vast array of tardigrades, too few species have been investigated so far; (2) the nature and origin of the tentacles of the onychophorans and of the sensory appendages of the head in several tardigrades: the assumption (Ramsköld, 1992) that ancestral Articulata had differentiated frontal appendages is mis-

leading: Ramsköld considered the fact that in most Cambrian species of "lobopods" one or more of the foremost pairs of appendages are somewhat differentiated with respect to the other walking appendages, but that does not mean that they are morphologically "frontal". It is obvious that any actively moving animal must explore the world in front of itself and, therefore, that it must cluster a good deal of its sensory apparatuses and associated nervous structures at its fore end. Nevertheless when we methodically consider the details of morphology and embryology of all the tentacles, antennae, lobes etc. scattered through the animal kingdom, it is clear that superficially similar structures have evolved independently a great many times. The Cambrian species had at most some small circumoral papillae, and some Cambrian animals had, apparently, one or two slightly modified anterior pairs of legs. New investigations into the development of the head region of both onychophorans and tardigrades may well be rewarding. This was shown by the results of Dewel and Dewel's (1996) investigations, who considered that the head region of the Tardigrada shows evidence of being the result of the concentration of three metameres. We suspect that the tentacles or antennae of living onychophorans have evolved as a specific adaptation to terrestrial environment in order to gather chemical and tactile information which could no more be mediated by water. Finally, though Lobopodans are rather rare fossils even in the richest Lagerstätten, it is curious that we have not yet unrecovered either larvae or juveniles (the suite of specimens of *Aysheaia* from the Burgess Shale has specimens of considerably different size, but none of them may be deemed a juvenile).

1.4 *Kerygmachela*

Kerygmachela kierkegaardi (Fig. 6) has been described so far (Budd, 1993) only from the lower Cambrian Sirius Passet fauna (North Greenland), which is probably the oldest Cambrian Lagerstätte so far discovered. Its morphology is still somewhat debated. In a preliminary lecture in London (April 1996), Budd gave some further details and restated his interpretation of the fossils (Budd, 1998). Some doubts, however, have been raised by other authors (Chen *et al.*, 1995) on

such an interpretation, especially concerning the supposed walking or inner branch of the legs. As may be seen from Figure 6, the animal is apparently a soft-bodied creature of moderate size, not much smaller than Cambrian Lobopoda, provided with a large pair of flexible and possibly grasping appendages in front and two long cerci. Whether the grasping appendages were lateral to the mouth or were fully preoral cannot be said. To the sides of the animal, there protrude 11 pairs of large flaps, but whether fringed or simply grooved, again, cannot be said. Small conic protrusions have been interpreted by Budd as *Peripatus*-like legs, while there is also the possibility that these structures were in fact dorsal and so comparable to the spiny platelets of *Xenusion*. Budd himself considers that the animal had some dorsal papillae, perhaps more strongly sclerotized than the rest of the tegument, and this is confirmed by Christensen (pers. comm.) who has seen the material. On the other hand, Conway Morris (pers. comm.) considers the existence of ventral appendages as probable. Budd considers that the lateral flaps were independent of the appendages, and were pleural-like folds comparable to those, in his interpretation, of some anomalocarids (as reconstructed by Whittington) and of *Opabinia*.

It appears that we have in *Kerygmachela* an early swimming predator, though it is also possible that, as an unidentified anomalocarid was present in the Sirius Passet fauna, in spite of its size we have here some advanced developmental stages of anomalocarids.

1.5 *Opabinia*

Several authors (Bergström, 1986, 1987; Hou *et al.*, 1995; Budd, 1996) place *Opabinia* close to the Anomalocarida. The characters assumed to be common to the two groups of taxa are presumed by Bergström and by Hou and coll. to be the following ones: the presence of segmentally arranged transverse sets of scales over the whole width of the dorsum, a simple intestinal canal extending from the mouth to a terminal anus, an interconnected pair of preoral grasping appendages resulting in a proboscis-like structure, and, possibly, a ring of sclerites surrounding the backward directed mouth. Moreover, these animals, basically following Whitting-

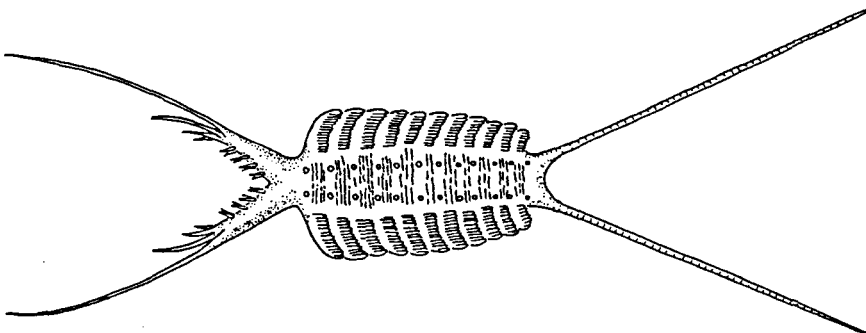


Fig. 6 - The Lower Cambrian *Kerygmachela kierkegaardi* Budd 1993, slightly modified.

ton's reconstruction (1975), appear to have been devoid of the more typical Arthropod synapomorphies. Finally, *Opabinia* and *Anomalocaris*, once again according to Whittington's reconstructions, would be both devoid of true appendages and appear to have swum by undulating some sort of lateral lobes. However, we consider that all these supposed synapomorphies either do not exist or are, at least, dubious, as we shall briefly discuss here.

We shall first see which is presently the more plausible interpretation of the morphology of this animal and, subsequently, we shall discuss its possible affinities.

Its head and general body structure is shown in Figure 7, the only feature not shown in the reconstruction being the mouth. The mouth of *Opabinia* is indeed directed backwards and, in some specimens, it looks as if it has a set of thin lines around it, but (1) according to the most recent materials published, in the anomalocarids the mouth was either directed ventrally or at most only slightly backwards; (2) the delicate lines seen around the mouth of *Opabinia* do not look at all like the strong denticulated platelets of anomalocarids, but rather suggest a distensible rim, which could accommodate fairly large preys, functionally such as occurs in a number of different phyla. The simple gut is obviously of no phylogenetic significance, it is most probably simply a primitive character and is anyhow shared with other animals, even in the Burgess Shale, such as unquestionable Arthropoda (e.g., *Leanchoilia*), Annelida etc. The occurrence of lanceolate lamellae across the dorsal side of *Opabinia* has been denied both by Briggs & Whittington (1987) and by Budd (1996). Finally, paired grasping appendages topographically preoral (to commit oneself to a definite judgement as to whether they were truly morphologically preoral, one should know their development) occur in different but unquestionable Arthropoda (e.g., *Leanchoilia*, *Alalcomenaeus*, *Actaeus* etc.), some of them being structurally much more comparable with those of anomalocarids than the proboscis of *Opabinia*.

Indeed, it is true that in a few instances (e.g., in the males of some anostracans), the antennulae are partly fused and form a curious frontal organ. Therefore we can not entirely rule out that the frontal proboscis of *Opabinia* derived from originally paired structures; yet it is anyway so radically different from the great raptorial appendages of anomalocarids that there is no reason to suppose that during its evolution there ever was a plesiomorph stage in any way comparable to the grasping appendages of anomalocarids or to their possible forerunners. On the other hand distinct terga are obvious in *Opabinia*, while they are either not extant or obscure in the Anomalocarida. As for the appendages, we are in a most controversial field. As shown by Fig. 7C-H, the different authors gave widely divergent interpretations. As a matter of fact, dismissing the reconstruction proposed by Simonetta in 1970 as obviously biased by the unconscious assumption that the animal was an

Arthropod and, therefore, should have had basically trilobitic appendages, the only really unbiased reconstruction is that by Whittington. Yet it is certainly wrong, at least in details. Indeed, both Bergström and Budd have independently shown, on the same specimens studied by Simonetta and by Whittington, that the "appendages" had fringes of lamellae; while Bergström locates them beneath pleural lobes, as in Simonetta's reconstruction, but not as part of a trilobitic leg, Budd comes back to Whittington's interpretation and considers it probable that they were dorsally attached to the "pleurae" or "flaps", along their fore margin, and credits *Opabinia* with true little legs of lobopod type. Budd's interpretation, however, by his own admission, is influenced by his interpretation of *Kerygmachela*.

Our present reconstruction (Fig. 7) is partly based on functional considerations. It seems indeed clear that swimming was accomplished by a sort of "jet propulsion", with water entering from the front of the animal and being expelled along the back margin of each flap or pleural lobe.

Contrary to anomalocarids and *Kerygmachela*, *Opabinia* was not a flat animal, because "flying" in water by the movement of laterally expanded "wings" was impossible. As it held its "flaps" more or less vertically, the sort of locomotion envisaged required that each "flap" was regularly ab- and adducted, with a slight rotation on its main axis, a little like an oar. Functional considerations cannot help to decide whether the branchial lamellae were dorsal or ventral to the "flaps", as their relationship to water currents would be the same. Comparative anatomy may be helpful. The study of the foremost pair of "flaps" appears to give some evidence that there were no fringes dorsal to it, but that the first bunch of fringes was located in the space between the first and second "flap". The three pairs of "rudder" flaps are obviously devoid of branchial fringes, and fringes were apparently present in the last pair of swimming "flaps" or "paddles". This seems more consistent with the hypothesis that the fringes were ventral.

The existence of short, stumpy ventral legs (whether lobopod-like, as claimed by Budd, or more "arthropod-like" is impossible to tell on the available material), does indeed make sense, as they would be needed to allow the animal to attach itself to some support when at rest.

As for the morphology of the head and especially of the proboscis, there is now a general consensus that the frontal organ was a flexible, superficially annulated structure, the extension of which was due to a hydraulic mechanism: the fossils clearly show that inside it there was a large cavity, which must have been filled with fluid and which may or may not have been in communication with body cavities. If it was continuous with other body cavities, the influx of liquid from the body increased pressure in the proboscis cavity and hence extended it. If the proboscis cavity was closed, then there must have been an intrinsic musculature in it

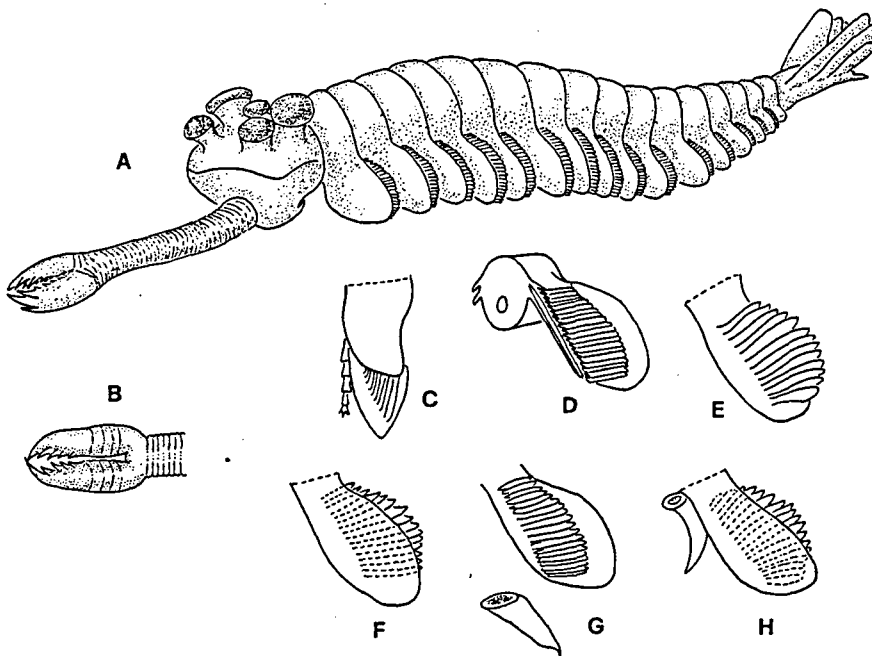


Fig. 7 - *Opabinia regalis* Walcott, 1912 (Middle Cambrian). A, the entire animal; B, dorsal view of the tip of the proboscis; C-F, successive reconstruction of the "flap-tergum"; C. Simonetta (1970); D. Whittington (1975); E. Delle Cave & Simonetta (1991); F. Bergström (1986); G. Budd (1996); H, our present interpretation.

to squeeze and straighten the organ. In either case, it is just possible, but most unlikely, that such a mechanism could be the result of fusion of two separate anlage, as should be expected if the structure derived from the fusion of paired structures. True enough, the grasping nails (Fig. 7B) at the tip of the proboscis appear to be in the horizontal plane (not in the vertical as suggested by Whittington), but this is a far cry from evidence that they are modified paired appendages. There is a denticulated movable pair of "fingers" supported by a bulbous structure that clearly housed the musculature acting them.

Finally a word on the eyes: the five large and certainly compound eyes, were placed on stumpy, apparently unmovable pedicles. This has no morphologic significance as eyes carried on pedicles occur in different Burgess Shale animals: *Sarotrocerus*, *Yohoia*, *Perspicaris*, *Actaeus*, and at least some anomalocarids, clearly belonging to widely diverging phyletic lineages.

The only real similarity between *Opabinia* and the anomalocarids appears to be the three lateral flaps bent upwards and functioning as stabilising or, possibly, steering mechanisms. However, the flaps themselves are arranged differently in the two groups, as in *Opabinia* each caudal flap overlies the more cranial one and vice versa in the anomalocarids, where, moreover, they are apparently absent in some genera. Their obvious functional value makes it likely that they are due to simple convergence.

It is scarcely necessary to dwell on possible comparisons between *Opabinia* and *Tullimonstrum*. Whatever the affinities of this last genus, the most reliable interpretation of its morphology is still that by Beall (1991) which shows that the two animals did not share any

common character as even the "proboscis" was morphologically entirely different in the two animals.

It is clear that there are still several obscure points in our interpretation of the morphology of *Opabinia*, which may be solved only by the evidence of new materials. Unfortunately it is not known whether new specimens have been discovered during these last years of exploration of the Burgess Shale and related quarries. To sum up, we feel that there is no sound evidence for grouping *Opabinia* with any particular group within the Articulata.

1.6 Anomalocarids (*Dinocarida*, *Radiodonta* of Collins, 1996)

This group, though it has a sufficiently homogeneous basic Bauplan, has been shown by recent discoveries to be not only rich in species throughout Lower and Middle Cambrian, but also much more morphologically varied than previously expected. One point, however, should be considered: one of us (Simonetta) in 1963, at a time when he was, wrongly, considering the spiny lamellae as belonging to *Sidneyia*, pointed out that isolated lamellae in the Burgess Shale showed a surprising variety (Fig. 8A) such that one could safely expect that several species were present. This may well hold true, but quite recently Hou *et al.* (1996), describing the appendages of the Arthropod *Kunmingella* (Fig. 8B), have shown that some of the forelegs were provided with spiny lamellae which, albeit very small, resemble in a surprising way some of the lamellae described by Simonetta in 1963! Therefore, if we consider that in the Middle Cambrian Burgess Shale there is a number of large bivalve arthropods whose appendages are un-

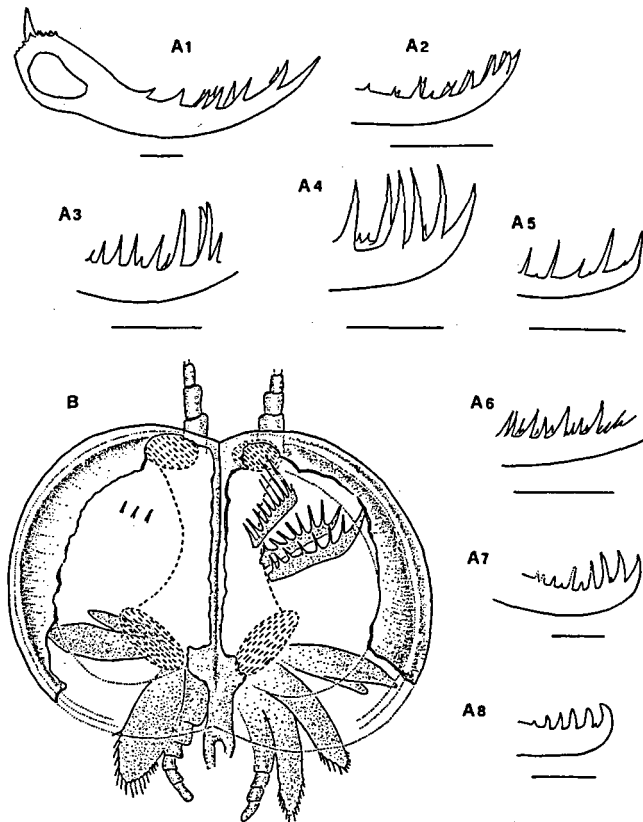


Fig. 8 - A1-8, isolated lamellae from the Burgess Shale figured by Simonetta (1963) (A1 certainly belonging to a specimen of *Laggania*), showing the variety of spinulation, indicative of different species, and B, the "crustacean" *Kunmingella maotianshanensis* Hou & Shu, 1983 (Lower Cambrian) after Hou *et al.* (1996), with the fore appendages markedly similar to some of the lamellae figured in A.

known and that some of them, e.g. *Carnarvon*, are extremely similar, size apart, to the valves of *Kunmingella* or of bradoriids, we must also consider the possibility that some of these spiny lamellae did not, in fact, belong at all to anomalocarids. Indeed years ago Collins showed at an International meeting in Camerino (1989) some large bivalve carapaces from the Burgess Shale system associated with spiny appendages suggesting anomalocarid affinities. As far as we know, reports on these specimens, which could provide some relevant evidence, have not yet been published.

After these premises, we may now turn to the anomalocarids proper: several species from localities in North America (Briggs & Mount, 1982; Briggs & Robison, 1984; Whittington & Briggs, 1985), Greenland (Budd, in press), Australia (McHenry & Yates, 1993), Poland (Dzik & Lendzion, 1988; Masiak & Żylinska, 1994), China (Hou & Bergström, 1991; Chen *et al.*, 1994), are still too poorly known for satisfactory comparisons: they only show that, at least since the earliest Cambrian, anomalocarids were a powerful and varied group of predators. Yet at least two species from the Burgess Shale and some from the Lower Cambrian of China are sufficiently

known to allow for a general assessment of this group. *Cucumericrus decoratus* from China, though poorly known, at least for some characters of the appendages clearly shows features of great interest (Fig. 10).

It is worth remembering here that when Walcott (1911a) described *Amiella ornata*, he regarded it as congeneric with Cambrian material from Yunnan, but apparently no one has reinvestigated the relevant material. Now, as shown by Whittington & Briggs (1985), with whom we concur, the holotype of *Amiella ornata* is probably an anomalocarid. Reinvestigation of the Chinese material quoted by Walcott would be worthwhile, as it may also disclose some interesting nomenclatorial problems. Figures 9 and 11 show our present reconstructions of some anomalocarid species.

We shall first note that, while quite varied in details, the general pattern of the large grasping appendages is a necessary consequence of the position of the mouth, whether it was facing backwards or simply downwards.

Even if we consider the size of the animals (there is a mouth ring of plates 20 cm across, which clearly shows that some species could easily exceed one metre in length and possibly reach up to two metres; see Briggs, 1994), the animals nevertheless needed a pair of appendages to handle the prey and bring it to the mouth. As the mouth faces downwards or backwards, such appendages must necessarily have become preoral, even if they may have originally belonged to the first postoral somite.

The mouthparts of anomalocarids are certainly highly significant: there clearly was an outer ring of "teeth", which can be either pushed apart or closed towards the centre of the mouth. They can, moreover, be rotated to some extent so as to protrude or retract their tips. Though we cannot be sure of the amount of such protrusion, there is no doubt that by their outer crown of teeth the anomalocarids could "bite" into their prey. Inside this outer crown, there were spiny, interlocking structures, which were not protrusible, but which did "chew" the food pushed inside by the biting teeth and by the raptorial appendages. If we consider that an at least partly extrusible mouth is the only possibility for any macrophagous animal in order to feed, unless it has a mouth either large enough to swallow its prey entire or can cut its prey into pieces and handle it properly with suitable appendages, more or less protrusible mouthparts must be expected to have been evolved independently several times. Therefore we think that comparison to other buccal apparatuses, such as suggested by Hou *et al.* (1995) in respect to that of *Kinorhyncha*, may be useful in terms of functional morphology, just as one can see functional analogies in respect to the mouthparts of many Echinoderms, but have no phylogenetic significance. Again, the inner lamellar structures of the buccal apparatus of the anomalocarids are functionally equivalent to the esophagean mill of several arthropods.

The appendages of the Anomalocarids are extremely

interesting in their great variety. In order to better understand their structure, we shall begin by considering those of *Parapeytoia* Hou *et al.* (1995) (Fig. 9C). Its walking appendages, on the one hand, are rather similar to those of typical arthropods and to the raptorial appendages of all anomalocarids: they have an inner branch made up of several more or less spiny articles. However, in the basal and dorsal region, the separation between the inner and outer, swimming and respiratory branch, is indistinct: the two branches merge in a large basal piece, strongly spinose on its free margin. Moreover the leg is not attached to the body by a true articulation, but by a wide strip of thin, finely folded cuticle. The outer branch, as said, largely merges into the basal segment, while distally, albeit less clearly than in *Anomalocaris saron* Hou *et al.*, 1995, it was laterally produced into a fringe of imbricating lamellae. As in the other anomalocarids, these outer branches are regularly imbricated with the adjoining ones. We cannot tell whether the outer branch only merged with the basal article of the leg or also with the pleural region of the body. Both in this species and in *Anomalocaris saron*, there were true distinct sternites, while the dorsal surface seems to have been covered by rows of thin blade-like scales.

Anomalocaris saron and *Parapeytoia yunnanensis* are the two anomalocarids most closely approaching

the structure of Arthropods. However, they diverge from arthropods in two critical features: the mouth structure and the dorsal side, which, instead of being covered by segmental terga, appears to have been extremely flexible throughout. We shall consider further on whether it is possible to suggest some hypothesis on the evolutionary morphology of such appendages.

We have fragmentary knowledge of *Cucumericrus decoratus* Hou & Bergström, 1995. However, some of its appendages are exceptionally well-preserved. These, while conforming with the overall plan of those of the previously discussed anomalocarids, are interesting as their segmentation into true articles only obtains in the more distal part of the leg, while proximally the leg is covered by irregular platelets or simply by a finely folded cuticle. One might obviously object that the only known specimen might be a freshly moulted one, so that the cuticle was not yet fully expanded and sclerotised. Though this cannot be entirely ruled out, the overall evidence of the fossil as described suggests that we have here a truly incompletely segmented appendage. The last Chinese species worth mentioning here (a still unnamed species of *Anomalocaris*; Chen *et al.*, 1994) is notable because it clearly has in addition to the three pairs of upturned stabilising flaps two long cerci, otherwise unknown among anomalocarids.

Returning to the two better known species from the

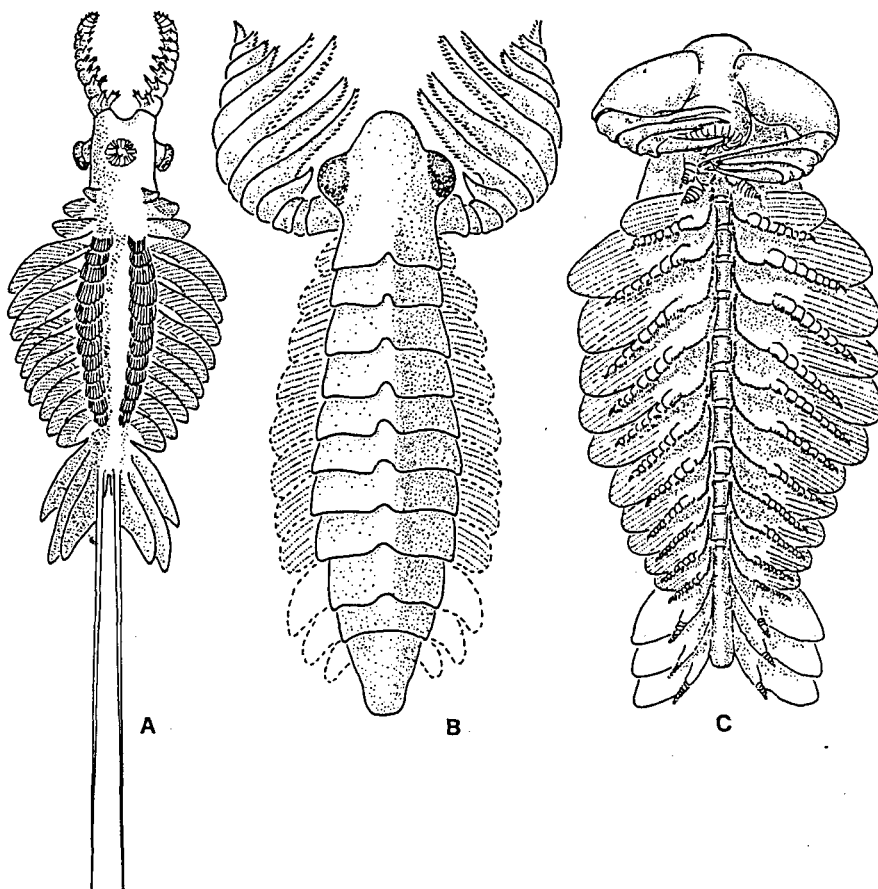


Fig. 9 - Three Lower Cambrian Anomalocarids. A, *Anomalocaris* sp. from China published by Chen *et al.* (1994); B, *Cassubia infercambriensis* (Lendzion, 1975), from Poland; C, *Parapeytoia yunnanensis* Hou *et al.*, 1995, from China.

Burgess Shale, *Anomalocaris canadensis* (Fig. 11A, B) appears to diverge largely from the Chinese species because its flaps are widely attached to the body, there is no trace of the ambulatory branch of the leg and the flap, though striated as in some Chinese anomalocarids, seems to have been strengthened by nervures or veins rather than being formed by lamellae. As already mentioned, the type of *Amiella ornata* Walcott, 1912 from the same locality as *A. canadensis* is most probably an anomalocarid, but it cannot be attributed to known species, and appears to confirm that also in these animals, the dorsum was covered by regular rows of hair-like structures. The fact that, while true sternites are known from some Lower Cambrian anomalocarids, others from the Middle Cambrian (*Laggania*) (Fig. 11C) are ventrally clearly segmented by rows of structures (that we shall discuss further on), but apparently lacked dorsal segmentation, supports the contention that there were no real terga, but that the dorsal surface was covered by regular rows of small weakly sclerified structures.

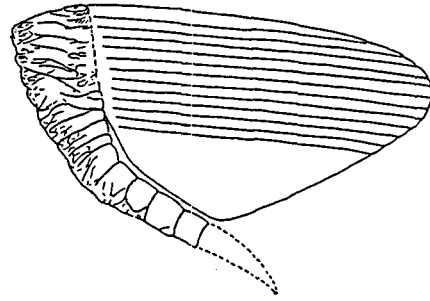


Fig. 10 - *Cucumericrus decoratus* Hou *et al.* 1995, showing the incomplete segmentation of the appendages.

The other Burgess Shale species (commonly known as *Peytoia nathorsti*, but which Collins (1996) holds should be named *Laggania*) diverges from *Anomalocaris* because (1) its raptorial appendages are similar to those of *Cassubia* or *Parapeytoia*; (2) there are no terminal stabilising, dorsally directed, rigid, specialised flaps; and (3) most significant, the swimming flaps are

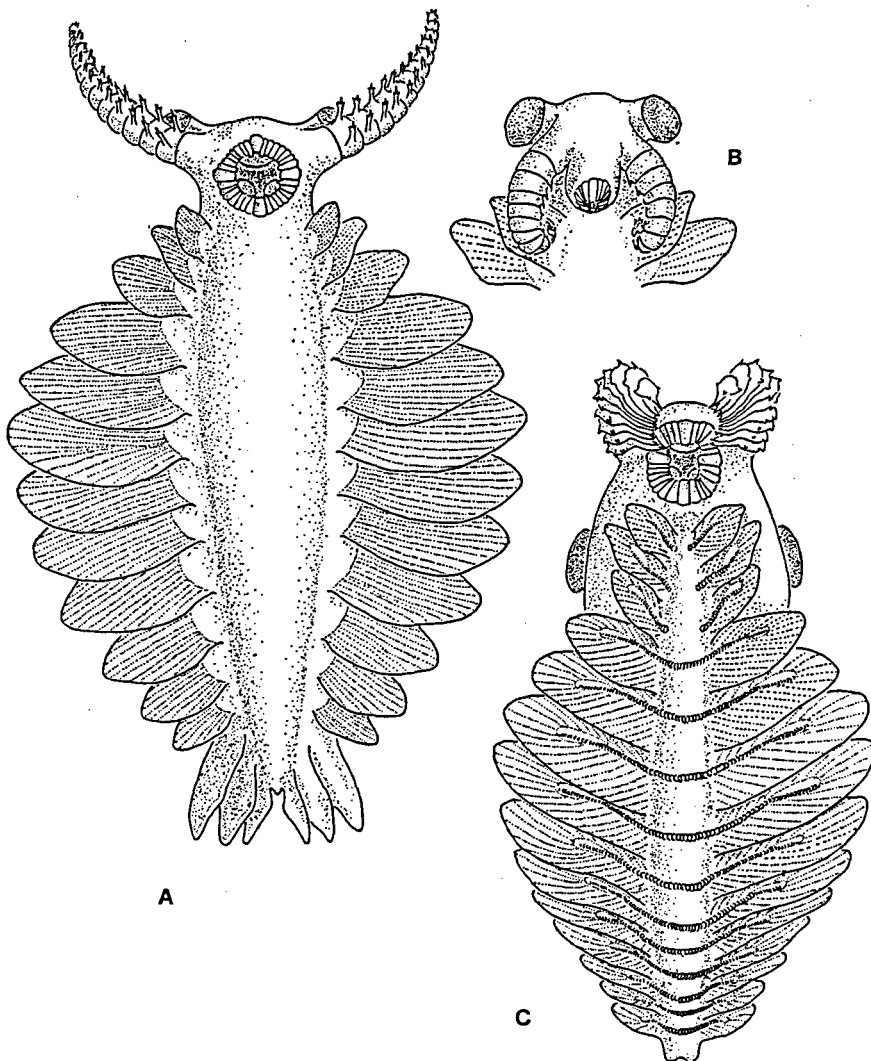


Fig. 11 - A-B, *Anomalocaris canadensis* Whiteaves, 1892; B, detail of the head from the ventral side; C, *Peytoia* (= *Laggania*) *nathorsti* (Walcott, 1911) (Middle Cambrian).

strengthened ventrally by a row of nodular structures (Fig. 11B). These rows, in the first three pairs of flaps stop at the base of the flap, leaving the sternal region free, while in the following appendages they form a continuous row across the body. They all end with a somewhat expanded tip and were apparently attached through their whole length either to the flap or to the body. We think that these structures are homologous to the inner branch of the legs of *Parapeytoia* and *Cucumericrus*. While this structure, which judging from its fossilization appears to have been strong, probably acted as a stiffening rod attached to the flaps, it may have been fringed by delicate elongated structures (they appear to be ventral and not dorsal as in Bergström's (1986) reconstruction. These latter structures may have been respiratory.

Is it possible to propose a balanced assessment of the phylogenetic significance of the anomalocarids? Until the discovery of the more arthropod-like Chinese species, hardly anyone would have doubted the judgement, that we advanced in 1982 (Simonetta & Delle Cave, 1982) when we gave the first preliminary description of these animals, and that was soon confirmed by the much more exhaustive study by Whittington & Briggs (1985), that these were the representatives of a new phylum. The new evidence points to a somewhat different conclusion: though the evidence is still too fragmentary for a definite judgement on whether the more arthropod-like or the more flap-like appendages are the more primitive, we have here a series of morphological stages ranging from entirely "un-arthropod" appendages, to "almost-trilobite-like" ones. They all, however, share two features: (1) their movements of promotion and remotion, when at all possible (e.g., presumably, in *Parapeytoia*), must have been largely linked with local turgescence and/or contraction of the body musculature (combined action of dorso-ventral and cranio-caudal muscles, together with hydraulic extension or muscular abduction of the distal part of the leg), rather than to rotation of the leg itself; (2) from the standpoint of functional morphology, these animals have no lateral sides: there is only a dorsal side, rather undifferentiated, and a ventral side, eventually extending into legs and flaps.

If we take into account the respective age of the Chinese and of the American species, the morphological evidence available to date can be interpreted as follows: by the end of the Precambrian or the Lowermost Cambrian the anomalocarid-arthropod stock had evolved appendages like those of *Cucumericrus* in the framework of a truly metameric body; at least in some species, possibly because of size, the mechanical requirements of leverage required the selection of sternites (among true arthropods the development of sternites is so varied and so obviously related with functional requirements that the same may well hold true for anomalocarids). If *Cucumericrus*-like appendages were comparatively primitive, they could not possibly work

as efficient hydrofoils like the "flaps" of the Middle Cambrian anomalocarids, but the transition between the two is both topologically and functionally possible, and the peculiar rows of nodular structures of *Laggania* may well be considered as a modified remnant of the "inner" branch of the appendages. Further discussion of the comparative morphology of anomalocarids and arthropods will be found in the section on "problems of general morphology".

1.7 True arthropods

Although the bottom Cambrian layers have, so far, yielded only trilobites (though we are not convinced that *Kleptothule rasmussenii* described by Budd (1995), is an unsclerified primitive Olenellid and that it really belongs within the Trilobita), the rich and varied arthropod faunas and the occurrence of anomalocarids through all adequately known Lower Cambrian faunas are conclusive evidence that true arthropods (and most probably true annelids) must have been extant by the close of the Precambrian, and that we may allow for the possibility of a very rapid radiation of arthropods in the terminal phase of the Precambrian, even though not all the Ediacaran and Tommotian faunas include arthropods. Throughout the Lower and Middle Cambrian, apart from typical trilobites, arthropods are represented by a range of morphological types, which may well include the direct ancestors of later, traditional classes and orders. These were slowly evolving (there seems to be no basic difference between the arthropods of the Lower and Middle Cambrian), and none had as yet acquired all the "diagnostic" features of the present living classes; while several other true arthropod taxa existed which do not fit into any later taxon, and other groups, broadly related to the two largest living phyla of the Articulata, were reasonably common and ecologically important.

It is notable that all the traditional phyla of the Articulata (Annelida, Tardigrada, Onychophora, Pentastomida and Arthropoda) were well-developed by the Middle Cambrian at the very latest and that only two "phyla" have become extinct since: anomalocarids and opabiniids, the latter being practically restricted to a very short period in the Middle Cambrian.

2. PROBLEMS OF GENERAL MORPHOLOGY OF "ARTICULATA"

We must now consider several important issues concerning the origin of the "Articulata". Let us first deal with the problem of the possible relationships of Anomalocarida and Arthropoda. Though the two may be related as suggested especially by the appendages of *Cucumericrus* and *Parapeytoia*, it does not seem possible to consider the anomalocarids either as arthropods or as representatives of a stock from which true arthropods may have arisen. Comparison between even the

most primitive mouthparts of any arthropod shows that the arthropod labrum cannot be identified in anomalocarids. The classical theory that the arthropod mouth derived from a terminal one overhung by a small epistomial lobe, and that it gradually rotated ventrally and backwards, thus being able to recruit the fore pairs of legs into the feeding apparatus, is obviously true. In the anomalocarid ancestors, the mouth was probably terminal, too, and the fact that there is apparently some variation in the amount of rotation in different genera, if definitely substantiated, may be taken as evidence for it. But the rotation must have followed the acquisition of the rows of platelets around it. The fact that this allowed for biting and chewing was morphologically an important step in evolution. On one hand any improving in grasping abilities of the first pair of paired appendages would turn the animals into efficient predators much earlier than any true arthropod, which had to develop a whole battery of appropriate appendages before it could deal with comparatively large preys, an evolutionary level which they reached only by the second half of the Middle Cambrian. On the other hand, the morphology of the appendages of Tardigrada and the large Lobopoda may be considered as belonging to a common pattern, while their differences, great as they are, are almost certainly due to the great difference in size of these animals; instead the appendages of the Cambrian Pentastomida are considerably more arthropod-like.

The long debated homologies between the arthropod-lobopod appendages and the parapodia, if any, will be really clear only when we have a better understanding of the dorsal side of the anomalocarids and of *Opabinia*. Indeed, the parapodia of annelids show a great morphologic plasticity, so that the basic difference between parapodia and arthropod-lobopod appendages (the parapodia being morphologically lateral and the arthropod-lobopod appendages being basically ventral) may not be as important as it appears *prima facie*.

It is also traditional to consider the Articulata as being both metameric and bilaterally symmetrical animals, we must then consider these characters. That these animals, as well as a number of Precambrian ones are segmented is clear, but whether they were strictly metameric in the traditional definition of being formed by bilaterally symmetrical segments is much less obvious as:

1) A number of Precambrian segmented animals appear to be irregularly and, sometimes, asymmetrically segmented, an apparently primitive condition as shown by the evolution of bilateral symmetry in Chordata (Simonetta & Insom 1993; Insom *et al.*, 1995). Indeed both undulating and metachronal locomotion in a perfectly symmetrical animal requires a rather advanced nervous system, while in an animal which either moves by revolving on its axis or that has its segments offset, right and left, a much simpler neural chain is sufficient, as there is no need to inhibit the contralateral half segment when one starts off.

2) Talk about symmetry and metamerism in living animals is, usually, misleading. Beklemishev (1969) commented that, in fact, sessile and benthonic animals needed larvae to disperse and the swimming larvae are either basically bilaterally symmetrical or, anyway, move in a spiral rotating on their cranio-caudal axis. However, a rotatory movement is compatible only with very small and simply structured animals. Be they benthonic or actively swimming, animals will be under a strong selective pressure for bilateral symmetry, while radial symmetry is usually a secondary feature in sessile, almost sessile, or purely planktonic organisms. Radial symmetry is, moreover, seldom complete. Functional considerations therefore dictate that a tendency towards bilateral symmetry and its subsequent perfection, are features of limited phylogenetic significance as they, just as metamerism, probably arose repeatedly during the early evolution of the Metazoa.

3) Several small, non parasitic, annelids have no coelomic cavities, nor any other internal or external segmentation, and some of them appear to be morphologically rather primitive. Nemertines, on the other hand show different degrees of approach to a "metameric" structure, culminating in *Annuloneurtes*.

4) It may be argued that spiral segmentation may well be primitive, and radial cleavage may even have evolved from a primitive spiral cleavage (but, as a rule, arthropods have no spiral cleavage).

5) As in living animals with external segmentation, usually, but not always, there is a metameric arrangement also of the internal organs; it is commonly assumed that segmented fossils were metameric. This is probably true in most instances; but, remembering that the orthodox concept of metamerism associates the serial repetition of organs with a serial arrangement of coelomic pouches and that the classic idea that syncoeloms in the Articulata are a specialised or secondary condition is probably at least partly false (as already mentioned, there are acoelomate annelids, and classical annelid coeloms appear tightly linked with given types of locomotion), we have no reason to assume that the internal structures of Cambrian articulates were metameric in the precise meaning of the word. Moreover, the typical coelomic cavities of annelids could evolve only as collagen was freely available and, therefore arthropods, whose connectives are very poor in collagen, cannot possibly have ever had a typical deutocoel.

As a matter of probability, we consider it as likely that in the late Precambrian an incompletely bilaterally symmetrical and metameric stock radiated into many branches, so that, at least during the Lower and Middle Cambrian, while some lineages approached the structures of later, more familiar taxa, a number lingered on in what were to be blind alleys, and most became extinct by the end of the Cambrian and possibly earlier. It will be only when we have a more complete understanding of both the primitive stem groups from which

later taxa emerged and of their contemporaries which left no issue, that we shall really be able to assess also the evidence that has been and is being gathered on living Articulata.

Again, a few final words on the controversial issue of the relationship of the Annelida to the Arthropods and related groups. While Eernisse (Eernisse *et al.*, 1992) has consistently advocated inclusion of the Annelida and Mollusca within a clade Eutrochozoa, exclusive of the arthropods, mainly on the basis of 18S rRNA, Dick (in press), on the equally good evidence of homeobox genes, stresses the relationship of annelids and arthropods, and Nielsen (1995) and Nielsen *et al.* (1996) envisage a clade inclusive of classical Articulata plus Mollusca. Extensive discussion and contributions by many Authors at the recent International symposium on the relationships of major Arthropod groups, held in London in April 1996 (published 1998, see Fortey & Thomas 1998), produced such conflicting results that "bedlam" would be the most appropriate definition (see also Budd, 1996b).

We have postponed until here all references to the more general problems dealt with by Budd (in his contribution on the morphology of *Opabinia*). As a matter of fact, as Budd and ourselves have developed our respective arguments on the basis of conflicting theoretical premises, comparison, not to say criticism, is practically impossible. Our basic attitude as comparative morphologists is to consider evolutionary sequences in terms of possible topological transformations and of the requirements of functional anatomy. In this perspective we do not regard as valid the procedures of cladistic analysis, which, vice versa, are used by Budd. Thence a comparison of our arguments and Budd's would automatically involve a lengthy and inappropriate discussion on the theoretical aspects of cladistics. We shall, therefore, simply call the reader's attention first to a recent and important paper by Morchio (1996), who has shown by an impeccable argument of pure logic, based on the implications of Watanabe's theorem, that any kind of systematic approach starting with definition of characters and comparison with selected outgroups will be biased, so that the choice of the characters and of the outgroups will dictate the result which will necessarily be purely conventional and subjective. Second: that, although there is a fair consensus that our current understanding of genetics, population dynamics and selection, do not allow us to expect as probable either dichotomous branchings or that the modes of evolution can justify recourse to criteria of parsimony, yet these are presumed in most analyses on the plea that if these assumptions are renounced, objective scientific discussion becomes impossible. This is certainly false, as apparently modal and other non-linear logics, though usually unfamiliar to biologists, may be used successfully to deal with evolutionary problems.

3. APPENDIX (by Alberto Simonetta)

In 1988, G. Sundara Rajulu (Sundara Rajulu & Gowri, 1988), then professor of Zoology at the University of Coimbatore (India), gave a very preliminary description of an animal, which he claimed to be a living marine Lobopod and compared it to the Cambrian *Aysheaia*. In successive years (Sundara Rajulu & Gowri, 1990a, b; 1991a, b; 1992) he supplemented his description with further brief notes.

Having, by chance, found a reference to the original description, I asked my friend and colleague of the Zoological Survey of India, Dr. J. K. Julka, to trace the original papers for me. This he did at considerable pains, as all the papers had been published in an almost unknown and since deceased journal: "*The Indian Zoologist*", unavailable either in the libraries of the Zoological Survey of India, or of Universities such as Delhi or Chandigar. Finally, having traced some of the papers and the whereabouts of Sundara Rajulu, I was able to contact him and I got the whole set of his contributions.

It was obvious that the descriptions were exceedingly poor, as were the illustrations, and even the rules of nomenclature had been largely ignored. Yet the animal looked really curious (Figs 12-13) show the main evidences as claimed by Sundara Rajulu. Moreover, as we now know how marine Tardigrada have persisted with little change through some 500 million years, how could one *a priori* exclude that some other marine lobopod survived? I thus proposed to Prof. Sundara Rajulu that he should come and visit me with the material, so that a better study could be done. At the same time, as, while tracing him, I had heard some quite unsavoury rumours concerning his scientific reliability and I had to go to India for other researches, I made up my mind to go first to see him and the material on the spot.

About three months before my visit to India, Sundara Rajulu suddenly died. Thanks to the help of Professor Manuvalaramanujam, who succeeded Sundara Rajulu as director of the department and who did his best to help me before and during a visit to Coimbatore, I have been able to find out: 1) that the original material was not collected by Sundara Rajulu himself, but by a respected high school teacher, who is not mentioned in the papers; 2) that N. Gowri was the wife of Sundara Rajulu and that hers is apparently a purely "complimentary" authorship; moreover she must be aware that her late husband tampered with the original material, as she has persistently refused on different pretexts, not only to show me the material, but even to meet me; 3) I got the precise collecting localities, which Sundara Rajulu had mentioned only approximately; 4) it is almost certain that the evidence on which Sundara Rajulu claimed that the cuticle of his "Lobopod" contains α -chitin is forged and that he actually sent for examination a sample obtained from an arthropod, this being a kind of trick that Sundara Rajulu repeatedly played on colleagues (Jayaraman, 1989). It appears that Sundara Raju-

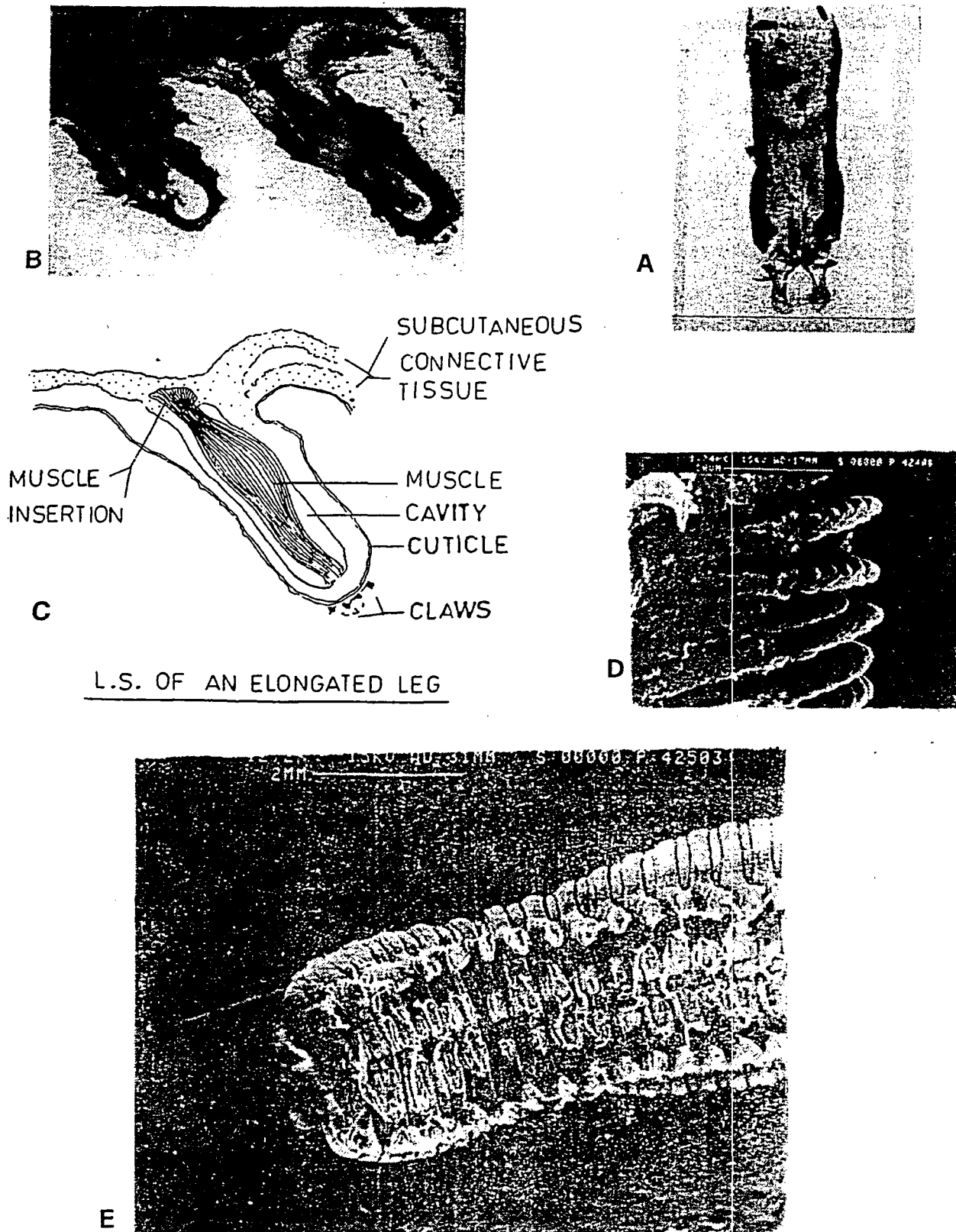


Fig. 12 - Some of the figures illustrating Sundara Rajulu's papers on the supposed "Lobopod worm" with some of the original explanations reported in *italics* between brackets. A-B; sections of the appendages [*longitudinal section of two legs of a lobopod worm, stained in Heidenbain's haemotoxylin*]; C, original interpretative drawing of Figure B; D, terebellid-like hooks of the appendages; E, ventral view of the forepart of the "Type" [*scanning electromicrograph of the ventral view of the holotype of the lobopod worm*].

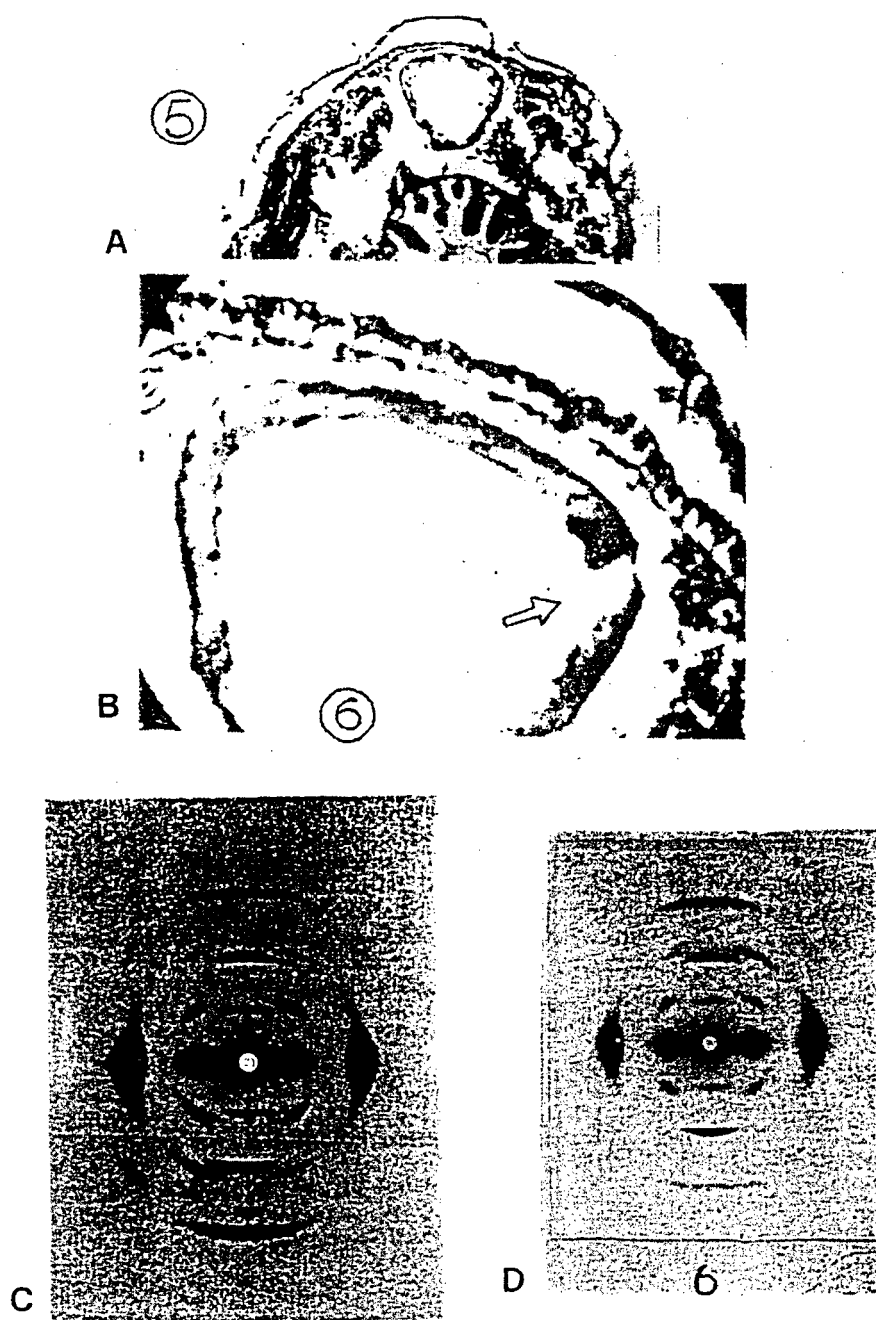


Fig. 13 - A-B, Sundara Rajulu's original illustrations of the transverse sections of the body of the "Lobopod animal" showing the dorsal vessel and the original explanations reported in italics between brackets [A. *transversal section of a trunk segment of a paratype of the lobopod worms showing the position of the dorsal vessel above the alimentary canal*; B. *transversal section of a trunk segment of a lobopod worm showing an ostium (arrow), stained in Heidenbain's iron-haematoxylin*]; C, diffractogram illustrating Karuppaswamy's paper, stated to prove the occurrence of β -chitin in a Pentastomid; D, diffractogram published by Sundara Rajulu as proof that the cuticle of his "Lobopod animal" had α -chitin in its integument.

lu published his papers in such a mini-journal as "*The Indian Zoologist*" in order to escape referees. On the other hand, when he died he was certainly busy trying to get additional specimens to bring with himself to Italy.

Dr. H. M. Walker, of the Department of Zoology of the University of Leicester, who took the originals of the scanning microscope photographs used by Sundara Rajulu in his papers, considers that the material she saw was probably a terebellid, artistically mutilated to look like a lobopod. This interpretation explains some, but not all the features seen in the photos published by Sundara Rajulu. One can see in the (horrible) published

slides, structures, especially of the appendages (Fig. 12D, E), which do not seem to correspond with any similar structure either in arthropods, annelids or onychophorans. Of these, the most curious is the arrangement of the musculature, which is apparently represented by only a strange retractor muscle, while the extension of the appendage would have been by to hydraulic pressure (Fig. 12A-C).

While there is no doubt that the late Sundara Rajulu made a practice of embellishing his evidence, some of his finds have been later validated by independent scholars (as, for instance on respiratory pigments in scutigermorphs). However, concerning alleged respira-

tory pigments of onychophorans, Sundara Rajulu himself admitted he to had tried to pass forged evidence on to colleagues.

As the original material has been either destroyed or anyway made unavailable by N. Gowri, it will be difficult to give a final reply to the question of whether there is anything of value under this smokescreen of tricks. Only new collections from the "type localities" might, perhaps, provide the final answer.

This controversial issue is further complicated by the quoted paper by Karuppaswamy (1977). This is an extremely short account of a diffractographic examination of a sample from the skin of *Raillietiella gowrii* and apparently shows that it contains β -chitin (Fig. 13C). However the paper was prepared in the Department of Zoo-logy of the University of Coimbatore, then chaired by Dr. Sundara Rajulu, whom the author thanks "for guidance and encouragement"; the species investigated is clearly named after Mrs. Gowri and the diffractogram (Fig. 13D) reproduced is apparently just the same material as that used by Sundara Rajulu in his later description of the "type" of the "Lobopod animal"! One does not want to challenge on such evidence the claim by Karuppaswamy, but unquestionably the highly suspicious dealings of his master require that Karuppaswamy's claim be carefully checked. Indeed, as sadly pointed out to me by Prof. Manuvalaramanujam, present director of Coimbatore's Department, it will be a hard job for him and for the present staff of the Department to recoup the scientific credit of their institution, so badly damaged by Mr. Sundara Rajulu.

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